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TAXONOMIC REVISIONS IN THE GENUS *ARCTOSTAPHYLOS* (ERICACEAE)

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Abstract

Changes are made in the nomenclature of species and subspecies in the genus *Arctostaphylos* (Ericaceae). In this study, the focus is on species found in the coast ranges of California. Changes are made in *A. nortensis* from the area around the Oregon border with California, in the *A. nevadensis* complex in the North Coast Ranges, in the *A. nummularia* complex of the north to central coast, in the *A. tomentosa* complex of the central coast to the Channel Islands, and in the *A. hookeri* and *A. pilosula* complex of the central coast. Also discussed are other changes presented elsewhere that will affect the *Arctostaphylos* treatment in the next edition of the Jepson Manual.

Key Words: *Arctostaphylos*, California, Ericaceae, new combinations.

The genus *Arctostaphylos* represents a quintessentially Californian complex of species that have radiated into a large number of soil types, climates, and plant communities. Philip V. Wells conducted the last major revisions of this genus (1968, 1987, 1988a, 1992, 1993, 2000). Wells developed a vision for the genus that included his typological view of taxa that idealized certain characteristics and overlooked important intra- and inter-population variation such as many bract or nascent inflorescence traits (Wells 1993, 2000). He proposed that a leafy-bracted, resprouting tetraploid complex was the core ancestral group (Wells 1987). For the last several decades we have also taken a systematic interest in this genus (most recently, Keeley and Massihi 1994; Keeley et al. 1997a, b; Markos et al. 1999; Vasey and Parker 1999; Hileman et al. 2001; Parker and Vasey 2004; Boykin et al. 2005; Keeley et al. 2007). These studies have led to a somewhat different view of *Arctostaphylos*, and based on our experience with the group, we propose a number of changes to the current treatment (Wells 1993, 2000) and provide our rationale for these changes.

Arctostaphylos nortensis

After examining specimens in herbaria, plus our own collections from the type locality, we were somewhat confused about the status of widespread populations of an *Arctostaphylos* taxon similar to *A. nortensis* (Wells) Wells but not quite matching the description. These populations were considered as either *A. nortensis* or hybrids referred to by Gottlieb (1968). Our specimens had the general pubescence and inflorescence characters we expected, but also contained glandular hairs. Following pressing and drying, these glandular hairs were somewhat cryptic in some of our collections. While not mentioned in the original description (Wells 1988b), later in his treatments of the genus Wells (1993, 2000) insists that this species has no glandular hairs on any organ. This led us to review the type specimen (*P. V. Wells and W. Knight 8186*, CAS). Here we found numerous glandular hairs, generally longer than most of the pubescence, somewhat different from those on our specimens, which were often shorter than the longest hairs. Nonetheless, we were impressed that the type contained the glandulosity we were seeing in the field. Consequently, we amend the description of *A. nortensis* to include presence of glandular hairs on the branchlets, and often on the petioles and edges of younger leaves. With this amendment, the "rare" status of *A. nortensis* needs to be re-evaluated because of the extensive stands of this taxon present in northern Del Norte County, California, and southern Oregon as well. At the same time, the difference in the type of glandularity among the type specimen, our collections, and Wells' descriptions (Wells 1993, 2000) suggests more research is required for a clearer understanding of this taxon. For example, cuttings from shrubs of the same area

as the type now growing in the Regional Parks Botanical Garden are non-glandular (Stephen Edwards, personal communication). Here we modify Wells' description to match his type specimen.

Arctostaphylos nortensis (P. V. Wells) P. V. Wells, emend. V. T. Parker, M. C. Vasey, J. E. Keeley, description to include usually with glandular hairs.—*Arctostaphylos columbiana* Piper subsp. *nortensis* P. V. Wells, Four Seasons 8(1): 50, 1988. *Arctostaphylos nortensis* (P. V. Wells) P. V. Wells, Four Seasons 9(2): 56. 1992. Type: USA, California, Del Norte Co., Gasquet Toll Road, near Gasquet on serpentinite, *Wells and Knight 8186* (isotype CAS).

Arctostaphylos nummularia Complex

As part of a molecular phylogeny of *Arctostaphylos* (Boykin et al. 2005; Wahlert 2005), *A. nummularia* A. Gray breaks into two groups, one from Mendocino County and northern Sonoma County and one from Marin County and Santa Cruz County. The southern populations, originally named *A. sensitiva* Jeps. (Jepson 1922), were transferred to a variety of *A. nummularia* by McMinn (1939). Further complicating this was Wells' (1989) separation of related populations in the north as *A. mendocinoensis* Wells. What has struck us about published descriptions of these plants is the failure to recognize a significant morphological distinction between the northern and southern populations, specifically a strikingly different bark characteristic. The Mendocino and northern Sonoma County populations have persistent bark, which on small plants retains a slightly red color, but as the plants age, the bark becomes grey and rough or shaggy. The plants in Marin and Santa Cruz counties retain the red, smooth bark throughout their lifespan, as is the case with the majority of *Arctostaphylos* species. McMinn (1939) noted that his conception of *A. nummularia* (which included *A. sensitiva* as a variety) included plants with exfoliating grey-brown or smooth reddish bark. Somehow, knowledge of this variation was lost in later treatments.

Morphologically, a gradual cline exists in characteristics between what Wells (1989) has named *A. mendocinoensis* and other collections of *A. nummularia* in Mendocino County, while southern populations from Marin and Santa Cruz Counties generally differ in characteristics from the Mendocino and Sonoma populations, such as the number of inflorescence branches. Both McMinn (1939) and Wells (1968 in Table 1) noted that the southern populations were generally more robust and less variable than those in the north. *Arctostaphylos mendocinoensis* is a diminutive, relatively prostrate shrub in harsh podsol soils in the pygmy forest which grades imperceptibly into upright shrubs (*A. nummularia*) in adjacent forest and maritime chaparral. As a consequence of the cline between *A. nummularia* and *A. mendocinoensis*, we propose submerging *A. mendocinoensis* as a subspecies of *A. nummularia*. *Arctostaphylos sensitiva* is an important member of maritime chaparral in southern Marin and the central to southern Santa Cruz Mountains, and because of the morphological and molecular disjunction between the northern and southern populations, we propose resurrecting *A. sensitiva* as a species inhabiting the southern region.

Arctostaphylos nummularia A. Gray subsp. **mendocinoensis** (P. V. Wells) V. T. Parker, M. C. Vasey, J. E. Keeley comb. nov.—*Arctostaphylos mendocinoensis* P. V. Wells, Four Seasons 8(3): 30. 1989. Type, USA, California, Mendocino Co., *P. V. Wells, I. Knight, W. Knight 11189* (holotype CAS).

The Arctostaphylos hookeri Complex

Taxonomic confusion has occurred among various clusters of species of *Arctostaphylos* that exhibit simple, elliptic, green leaves. Characters that separate them, such as fruit or nascent inflorescences, were not emphasized early in the taxonomy of *Arctostaphylos*. Wells (1968, 1993, 2000) took 5 of these simple green-leaved taxa and submerged them as subspecies of *A. hookeri* G. Don. *Arctostaphylos hookeri* was one of the earliest named manzanitas (by George Don in 1834), a distinctive endemic of stabilized dunes and upland sandstone habitats in the Monterey area, an area collected by early explorers in the 1800's. The next taxon named from Wells' *A. hookeri* complex was *A. montana* Eastw. (Eastwood 1897), a Marin County serpentine endemic. McMinn (1939) considered this to be a northern population of *A. pungens* and submerged it into *A. pungens*. He mentioned that, without inflorescences, some of the smaller specimens of *A. montana* are difficult to separate from the more erect forms of *A. hookeri* (McMinn 1939). Munz (1958) resurrected *A. montana* as a variety of *A. pungens*. Eastwood (1905) also named *A. franciscana* Eastw., an endemic shrub formerly abundant in serpentine areas in San Francisco. This species suffered a relatively similar fate as did Eastwood's *A. montana* Eastw. because McMinn (1939) submerged it into *A. hookeri*, and later Munz (1958) resurrected it as a subspecies of *A. hookeri*. *Arctostaphylos hearstiorum* Hoover & Roof was first described by Hoover and Roof (1966) and is known only from coastal grasslands of the Hearst Ranch near San Simeon. Finally, a remaining individual of a formerly more

extensive population from serpentine areas of San Francisco found by Peter Raven was named *A. hookeri* subsp. *ravenii* (Wells) by Wells (1968). The range of natural variability of this taxon is unknown.

In one of his first revisions of the genus, Wells (1968) lumped the three serpentine endemic taxa from the northern San Francisco Peninsula and southern Marin with the two taxa from the Monterey and San Simeon area, creating his *Arctostaphylos hookeri* complex. *Arctostaphylos hookeri* subsp. *montana* (Eastw.) Wells and *A. hookeri* subsp. *ravenii* are both tetraploid, serpentine endemic species. While some similarities exist, they differ from *A. hookeri* subsp. *hookeri* in a number of characters, but principally with regard to the nascent inflorescences and fruit. Morphologically similar to the two serpentine endemics is the diploid, *A. hookeri* subsp. *franciscana* (Eastw.) Munz, also a serpentine endemic, but extirpated in the wild. *Arctostaphylos hookeri* subsp. *hookeri* is a diploid endemic to the Monterey region and is found on sandy or clay soils. *Arctostaphylos hookeri* subsp. *hearstiorum* (Hoover & Roof) Wells is a diminutive taxon, similar in structures to *A. hookeri* subsp. *hookeri*, but much smaller; the plant is also completely prostrate, and is found in grazed grassland areas on mostly clay soils.

Markos et al. (1999) examined this group using molecular markers, principally from the nuclear ribosomal ITS region. The result was that the three northern taxa, *A. hookeri* subsp. *montana*, *A. hookeri* subsp. *franciscana*, and *A. hookeri* subsp. *ravenii*, were not closely related to the two more southerly distributed subspecies, *A. hookeri* subsp. *hookeri* and *A. hookeri* subsp. *hearstiorum*. These results have been substantiated in later work with more species (Boykin et al. 2005; Wahlert 2005), and supports separation of the northern taxa from *A. hookeri*. As a result, we propose to resurrect *A. franciscana* and *A. montana* at species rank and to make a new combination for subsp. *ravenii*. We provide the following treatment and key to this revised complex:

Arctostaphylos montana Eastw. subsp. **ravenii** (P. V. Wells) V. T. Parker, M. C. Vasey, J. E. Keeley, comb. nov.—*Arctostaphylos hookeri* subsp. *ravenii* P. V. Wells, Madroño 19: 200, 1968. Type: USA, California, San Francisco Co., on serpentinite in the Presidio, *P. V. Wells 2767* (holotype UC).

Key for the former *Arctostaphylos hookeri* complex:

1. Immature inflorescence inconspicuous, small, often dark raceme (rarely with one branch), leaves shiny green, elliptic to diamond-shaped (*A. hookeri*)
   2. Plants generally erect shrubs (>0.5 m in height), leaves narrowly to broadly elliptic, 2–3 cm L, 1–1.5 cm W . . . . . *A. hookeri* subsp. *hookeri*
   2′ Plants strongly prostrate shrubs (<0.25 m in height), leaves), narrowly elliptic to diamond-shaped, quite small (0.8–1.2 cm L; 0.4–0.7 cm W) . . . . . *A. hookeri* subsp. *hearstiorum*

1′ Immature inflorescence prominent and conspicuous, congested umble or panicle usually with several branches, leaves dull green, obovate to round-elliptic
   3. Fruits generally 6–8 mm wide, habit variable (may be erect), leaves not orbicular
      4. Leaves round-elliptic, 1–2.5 cm L, 1–2 cm W, young twigs white tomentose . . . . . *A. montana* subsp. *montana*
      4′ Leaves narrow elliptic, 1.5–2 cm L, 0.5–1 cm W, young branchlets gray tomentose. . . . . *A. franciscana*
   3′ Fruits generally 4–5 mm wide, plants always prostrate, leaves orbicular, 1–2 cm L, 1–1.5 cm W . . . . . *A. montana* subsp. *ravenii*

The Arctostaphylos tomentosa Complex

Wells' (1987) vision that the *Arctostaphylos tomentosa* (Pursh) Lindl. complex is the core ancestral group of taxa in *Arctostaphylos* is based on several characters relatively atypical in the genus, such as bifacial leaves, leafy bracts, shreddy persistent bark, and resprouting ability, which are mostly shared among outgroup sister genera in the subfamily Arbutoideae (e.g., *Arbutus*, *Comorostaphylis*, *Xylococcus*, *Ornithostaphylos*, and *Arctous*), and consequently these characters are hypothetically basal within *Arctostaphylos*. However, whereas bifacial leaves and resprouting ability are shared among these other closely related genera, they are in general characterized by scaley bracts (not leafy) and at least three genera have members with smooth bark rather than persistent shreddy bark (i.e., *Arbutus*, *Ornithostaphylos*, and *Arctous*). Further, *A. tomentosa* taxa are all tetraploid in a genus dominated by diploid species and a more parsimonious hypothesis is that they are derivative rather than ancestral, even though containing a cluster of potentially ancestral characters. These taxa have probably resulted from hybridization between more basal diploid species. One model is that they are allopolyploids that originated from crosses similar to the documented origin of *A. mewukka* Merriam (Schierenbeck et al. 1992).

In our view, Wells also did not adequately consider the pattern and range of variation within this complex. He weighted very heavily the presence of a basal burl and bifacial leaves with few or no stomata on the upper surface, traits that are found in all taxa within the complex. But, he did not give adequate weight to the fact that different subspecies vary markedly with

respect to bark characteristics of the older stems: some have grey shreddy bark and others have smooth red bark. In addition, his typological concept of this complex also did not adequately appreciate the extent of population variation in other characteristics; for example, he asserted that leafy bracts associated with the nascent inflorescences were similar throughout the complex. Our studies fail to support Wells' view as we have observed that bract characteristics, although commonly consistent across populations of other species in the genus, exhibit extraordinary variation within these tetraploid species. Our studies reveal that those subspecies with red, smooth bark tend to have most, but not all, populations displaying smaller scale-like bracts, while those with shreddy bark tend to have most populations with leafy bracts. These inconsistencies have provided considerable confusion in the field for identifying these taxa.

We propose that dividing Wells' *A. tomentosa* complex into two species complexes, one group of taxa with grey, shreddy bark and another with red, smooth bark, yields a taxonomy that reflects population patterns with geographic continuity suggestive of more logical phylogenetic relationships. The gray, shreddy bark taxa comprise one cluster that is restricted to the Monterey region and sparingly down the coast to San Luis Obispo County. The red, smooth barked taxa form another group that dominates the Santa Cruz Mountains, ridges of the east side of San Francisco Bay, inland to Mt. Diablo, south into the Gabilan Mountains, and north to southern Napa County. The latter complex is also distributed in isolated populations from Monterey to Santa Barbara Counties, and on the Channel Islands.

Based on the type specimen, the name *A. tomentosa* (Pursh) Lindl. (Pursh 1814; Lindley 1836) rightly belongs to the grey, shreddy bark group in this complex. Young twigs on *A. tomentosa* are short hairy, with similar hair on the lower surface of the leaves, often thinning with age. On subsp. *bracteosa* (DC.) Adams, twigs are also short hairy, and differ from subsp. *tomentosa* by also having long gland-tipped bristles, sparsely so on the lower surface of the leaves. Another population of a member of the *A. tomentosa* complex can be found in Monterey County, subsp. *hebeclada*, originally considered by DeCandolle (1839) as a variety of *Andromeda bracteosa* (treated here as subsp. *bracteosa*); these populations were treated at a level below subspecies by Wells. Eastwood (1934) classified it as a variety of *Arctostaphylos bracteosa*, while later McMinn (1939) named it a variety of *A. tomentosa*. Although distinctively glabrous on its lower leaf surfaces and lacking glandular bristles, this taxon was submerged in the Jepson treatment by Wells (1993). Twigs are sparsely short hairy. Aside from its gray, shreddy bark, it is very similar to *A. crustacea* ssp. *rosei*. Separating the *A. tomentosa* and *A. crustacea* complexes provides the opportunity to effectively distinguish between these two taxa. Populations of subsp. *tomentosa*, subsp. *bracteosa*, and subsp. *hebeclada* are all restricted to Monterey County, from Fort Ord to Carmel Valley, with subsp. *tomentosa* sparingly found farther south down the coast. The final member of the *A. tomentosa* complex is subsp. *daciticola* P.V. Wells, only found near Morro Bay on the volcanic peaks inland a few kilometers. Twigs are short hairy but also have longer non-glandular, white bristles. Lower leaf surface is tomentose to smooth with age.

Arctostaphylos tomentosa (Pursh) Lindl. subsp. **hebeclada** (DC.) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Andromeda bracteosa* DC. var. *hebeclada* DC., Prodr. 7(2): 607, 1839. *Arctostaphylos bracteosa* DC. var. *hebeclada* (DC.) Eastw. Leafl. W. Bot. 1:122. 1934. *Arctostaphylos tomentosa* (Pursh) Lindl. var. *hebeclada* (DC.) J. E. Adams ex McMinn. Man. Calif. Shrubs, 412. 1939. Type: USA, "Nova California", *Douglas 1524* (G-DC).

The red, smooth bark group includes two taxa named in the same early publication by Eastwood (1933), *A. crustacea* Eastw. and *A. rosei* Eastw. We have chosen the former taxon because of its priority within the publication. *Arctostaphylos crustacea* also has a wider distribution; Eastwood's description was originally based on specimens from the San Francisco area, Moraga Ridge and Grizzly Peak in the eastern side of the San Francisco Bay, and various places in the Santa Cruz Mountains. Twigs on this taxon are short hairy with long bristles, sometimes with glands on the bristles. The lower leaf surface is sparsely hairy but thins with age. This subspecies is distributed from southern Napa County, the hills on the east side of SF Bay over to Mt. Diablo and south to the Gabilan Mountains. It is also found throughout the Santa Cruz Mountains south to Monterey. Isolated populations range near the coast to the Channel Islands. Subspecies *rosei* differs by having twigs that are short hairy while leaf surfaces are smooth and glabrous. Flower pedicels and ovary are tomentose. Several small populations of this taxon occur along the Big Sur coast, however, the type locality is from the dunes of western San Francisco, now reduced to two known individuals.

An additional member of this complex is subsp. *crinita*. Some taxonomic confusion has existed with the name of this taxon. McMinn (1939) used this name based on Adams' dissertation, but later Adams (1940) called it *Arctostaphylos crustacea* var. *tomentosiformis*. Wells

(1968) originally followed Adams and used the subspecific name *tomentosiformis*, but in a later treatment (Wells 1987), following clarification by Gankin (1971), Wells switched to *A. tomentosa* subsp. *crinita*. This taxon is quite similar to *A. crustacea*, except that it is densely hairy on the lower surface of the leaves, and even sometimes is hairy on the upper surface as well. Its distribution is primarily in the southern Santa Cruz Mountains.

Three subspecies are found in southern California. Narrowly restricted to the Purissima Hills north of Lompoc in Santa Barbara County is subsp. *eastwoodiana*, associated with an outlying population of *Pinus muricata*. While the twigs on this plant are sparsely short hairy, leaf blades are smooth and glabrous, as is the pedicel and ovary. Although morphologically similar to subspecies *rosei*, in subsp. *eastwoodiana* the ovary is glabrous, while tomentose in subsp. *rosei*. Generally restricted to Santa Rosa and Santa Cruz islands is subsp. *insulicola*, although some individuals have been found in the southern Santa Cruz Mountains as well. Twigs are generally short hairy and leaves sparsely tomentose on the lower surface. Subspecies *subcordata* is another taxon restricted to Santa Cruz and Santa Rosa Islands. Twigs petioles, rachises and bracts are densely glandular hairy, often with longer glandular hairs.

Resurrecting *A. crustacea* requires a change in the names of many of the subspecific taxa, and here we provide an accounting of those taxa separated into *A. crustacea*, as well as a key to distinguish among the subspecies of both *A. tomentosa* and *A. crustacea*.

Arctostaphylos crustacea Eastw. subsp. **crinita** V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos tomentosa* (Pursh) Lindl. var. *crinita* Adams ex McMinn, Man. Calif. Shrubs, 412, 1939. *Arctostaphylos crustacea* Eastw. var. *tomentosiformis* J. E. Adams, J. Elisha Mitchell Sci. Soc. 56: 54. 1940. *Arctostaphylos tomentosa* (Pursh) Lindl. var. *tomentosiformis* (J. E. Adams) Munz, Aliso 4: 95. 1958. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *tomentosiformis* (J. E. Adams) P. V. Wells, Madroño 19: 198. 1968. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *crinita* (J. E. Adams) Gankin, Madroño 21: 148. 1971.—Type: USA, California, Santa Cruz Co., Bonny Doon Ridge, head of Liddell Creek, *J. E. Adams 928* (holotype UC).

Arctostaphylos crustacea Eastw. subsp. **eastwoodiana** (P. V. Wells) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *eastwoodiana* P. V. Wells, Madroño 19:197. 1968.—Type: USA, California, Santa Barbara Co., on diatomite, summit of La Purissima Ridge, *P. V. Wells 610672* (holotype UC).

Arctostaphylos crustacea Eastw. subsp. **insulicola** (P. V. Wells) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *insulicola* P.V. Wells, Madroño 19:197. 1968.—Type: USA, California, basaltic rocks above Pelican Bay, Santa Cruz Island, *P. V. Wells and J. B. Roof 5467*, (holotype UC).

Arctostaphylos crustacea Eastw. subsp. **rosei** (Eastw.) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos rosei* Eastw., Leafl. W. Bot. 1:77. 1933. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *rosei* (Eastw.) P. V. Wells, Madroño 19: 198. 1968.—Type: USA, California, San Francisco Co., on the hills bordering Lake Merced, *L. S. Rose 33037* (holotype CAS).

Arctostaphylos crustacea Eastw. subsp. **subcordata** (Eastw.) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos subcordata* Eastwood, Leafl. W. Bot. 1:61, 1933. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *subcordata* (Eastw.) P. V. Wells, Madroño 19: 198. 1968.—Type: USA, California, Santa Barbara Co., Santa Cruz Island, *J. T. Howell 6335* (holotype CAS).

KEY FOR THE *ARCTOSTAPHYLOS TOMENTOSA*/*A. CRUSTACEA* COMPLEX OF ERECT PLANTS WITH PROMINENT BURLS, BEARING STOMATA ONLY ON THE LOWER SURFACE OF THE LEAVES:

1. Lower stems grey, shreddy barked
   2. Twigs densely short pubescent with long glandular bristles . . . . . *A. tomentosa* subsp. *bracteosa*
   2′ Twigs densely pubscent but lacking long bristles with glands
      3. Twigs with long bristles above a short pubescence . . . . . *A. tomentosa* subsp. *daciticola*
      3′ Twigs lacking long bristles above short, dense pubescence
         4. Lower leaf surfaces densely pubescent . . . . . *A. tomentosa* subsp. *tomentosa*
         4′ Lower leaf surfaces glabrous or sparsely pubescent. . . . . *A. tomentosa* subsp. *hebeclada*

1′ Lower stems smooth, reddish barked
   5. Twigs with dense short pubescence and long glandular bristles . . . . . *A. crustacea* subsp. *subcordata*
   5′ Twigs with dense short pubescence but generally lacking long glandular bristles
      6. Twigs with long, non-glandular bristles above a short pubescence
         7. Lower leaf surfaces glabrous or sparsely pubescent. . . . . *A. crustacea* subsp. *crustacea*

7′ Lower leaf surfaces densely pubescent, sometimes less so on upper side . . . . . *A. crustacea* subsp. *crinita*

6′ Twigs with dense short pubescence, lacking long bristles

8. Lower surface of leaves glabrous

9. Pedicels and ovary short hairy . . . . . *A. crustacea* subsp. *rosei*

9′ Pedicels and ovary glabrous . . . . . *A. crustacea* subsp. *eastwoodiana*

8′ Lower surface of leaves persistently short hairy . . . . . *A. crustacea* subsp. *insulicola*

Other Considerations of the Current Jepson Manual Treatment

Further changes expected in the upcoming Jepson treatment include the following observations: Revision of the *A. glandulosa* subspecies (Keeley et al. 2007); range extension and addition of two burl-forming subspecies of *A. parryana* (Keeley et al. 1997b); removal of *A. peninsularis* Wells (from the state and inclusion of *A. rainbowensis* Keeley and Massihi [1994]); inclusion of *A. gabilanensis* (Parker and Vasey 2004), a new species from the southern Santa Cruz Mountains and a new subspecies of *A. patula* from the Sierra Nevada (Vasey and Parker in review). We also propose 3 additional revisions that follow.

When Wells (1968) published a new subspecies of *A. pilosula* Jeps., viz. *A. pilosula* subsp. *pismoensis* Wells, his description of *A. pilosula* subsp. *pismoensis* was of plants with leaves greener and more elliptic than those of the nominate subspecies from the type locality. Later, Knight (1989) changed the status and name of *A. pilosula* subsp. *pismoensis* to *A. wellsii* Knight. In Knight's article, he asserted that *A. wellsii* differs from *A. pilosula* in 17 morphological features that he listed. We examined the types of both *A. pilosula* (*A. E. Wieslander 552*, holotype UC) and A. *pilosula* subsp. *pismoensis* (*P. V. Wells 23*, holotype UC; cited as the type for *A. wellsii* in Knight [1989]), as well as a number of additional collections from the Atascadero region, Pozo Summit, Pismo Beach area, and sites inland. Patterns of variation and similarity among these collections calls into question the distinction between these taxa. A major problem is that most of the characters listed by Knight (1989) for *A. wellsii* actually better describe the type specimen for *A. pilosula*, specifically, twig, rachis and petiole hispidity, bract shape, density of ciliate hairs on bracts, and other characters. Other characters listed by Knight (1989) are quite variable among all populations, sometimes even within individuals, such as whether the filaments are glabrous or hairy at the base. In short, the characters used by Knight (1989) to segregate out *A. wellsii* do not differentiate collections from the type of *A. pilosula*. There are morphological trends, such as individuals with ovate to oblong-ovate leaves and much more glaucous hue being found at Pozo Summit, but on the whole, we find it difficult to separate these two taxa.

When the range of *A. pilosula* and *A. wellsii* as a whole is considered, plants in the northern part of the range at lower elevations (e.g., Atascadero to Santa Margarita) as well as in the southern part of the distribution (e.g., Price Canyon, areas around Huasna Road and Lopez Road) are essentially identical in morphology. Most individuals at Pozo Summit do appear to have rounder, whiter leaves, suggesting introgression with *A. glauca*, but numerous collections from either side of the summit demonstrate a mosaic of combinations, including individuals that would key out to *A. wellsii*. Strikingly, many collections at UC and JEPS from the Pozo Mountain region of *A. pilosula* are annotated by Knight with statements such as 'not typical for *A. pilosula*', and in those collections the leaves are more elliptic and greener than he perhaps was expecting for the location. Accordingly, we are submerging *A. pilosula* ssp. *pismoensis* and *A. wellsii* into *A. pilosula*.

Gankin and Hildreth (1988) published a new taxon from high elevation sites in the North Coast Ranges called *Arctostaphylos knightii* Gankin & Hildreth, a plant very similar to *A. nevadensis* except that it possessed burls and could resprout after fire. Wells (1988) transferred this taxon to subspecific status within *A. nevadensis*, but with his later treatments (Wells 1993, 2000) submerged it into *A. nevadensis*, considering it a hybrid. The considerable range of this taxon, and its large populations in some areas requires reconsideration. On the serpentinized peridotite areas at the California-Oregon border that were burned in the Biscuit Fire in 2002, for example, an extensive population of *A. nevadensis* subsp. *knightii* is resprouting and reestablishing its population. This population was throughout the areas we visited in Del Norte County, which makes it difficult to imagine this as an occasional hybrid between two parents, one of which does not occur at that elevation. Consequently, we recognize this subspecies as a valid entity as a subspecies of *Arctostaphylos nevadensis*.

Another entity deserving more attention is *Arctostaphylos pacifica* Roof, a burl-sprouting prostrate plant found on San Bruno Mountain in San Mateo County described by Roof (1962). This plant has been relegated to hybrid status by Wells (1993, 2000) within his treatment of *A. uva-ursi*. The problem with that hypothesis is that the presence of one parent on San Bruno Mountain, *A. glandulosa*, cannot be confirmed. We have

collected specimens from all the large burl-formers on San Bruno Mountain, and they represent good examples of *Arctostaphylos crustacea* subsp. *crustacea*, (with some glandulosity on several individuals). Among our collections, only two individuals of *A. crustacea* have any stomata on the upper surface and the density is considerably less than that of the lower surface. *Arctostaphylos pacifica*, however, is isofacial in stomatal density, as well as having a burl and a unique leaf condition (serrulate margins) among mature leaves; these characters do not support a hybrid origin for *A. pacifica* between *A. uva-ursi* and another San Bruno Mountain manzanita unless the characters are transgressive. Determining the chromosomal count of this taxon would be an initial first step toward understanding its relationships. However, given its distinct suite of characters and the unlikely assumption that it is a local hybrid (between parents currently in the vicinity), we resurrect this taxon as a valid species.

Other studies are ongoing for this complex genus and additional changes might be expected in the future. A number of plants have disappeared in more recent treatments, for example, because they have been considered hybrids, generally without any evidence being provided. Most of these we think deserve more investigation, such as a plant described by Howell (1945) as *Arctostaphylos cushingiana* Eastw. forma *repens* J. T. Howell. In Howell's article, he describes the near prostrate habit of this plant being *A. cushingiana* selected by ecological conditions of the habitat and even specifically dismisses the possibility of hybridization. Later, in a table of chromosome counts in the genus, Wells (1968) classified forma *repens* as a hybrid form indicating his interpretation that Howell bases his name on hybrid individuals. In his later treatments, he includes *A.* × *repens* within his treatment of *A. uva-ursi*, in contrast to Howell's interpretation (e.g., Wells 2000) of forma *repens* being derivative of *A. cushingiana* (*A. glandulosa* subsp. *cushingiana*). What strikes us as most incredible about the taxonomic shuffling of Howell's forma *repens*, is that Wells (1968) provides a diploid chromosome count for it, even though he describes it as of hybrid origin from two tetraploid parents; we know of no reasonable genetic process by which this could happen. We are in the process of re-examining the ploidy level of this entity. If it is in fact a diploid, then it could well represent a distinct entity worthy of taxonomic recognition.

Other complexes require additional attention in the future. Two obvious ones are the *A. uva-ursi* complex and the *A. manzanita* complex. Recent work suggests that many of the characters in *A. uva-ursi* are variable and not taxonomically informative (Rosatti 1987), and some molecular work indicates the close relationship among the various populations (Wahlert 2005). Its widespread distribution and patterns of morphology and ploidy levels suggest an interesting history that deserves more attention. Similarly, the *A. manzanita* complex is widespread and variable within California. Any new treatment of these complexes will require a better understanding of evolutionary relationships among their taxa and the role of hybridization in their origin.

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